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Decomposition studies on *Pinus taeda* forest
II. Decomposition of leaf litter[1]

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With 4 figures

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1. Introduction

Rates of litter breakdown are dependent on the microbial biomass which has invaded it, temperature, moisture and chemical composition of the litter which govern the microbial activity (Melin 1928; Harrison 1971; Fogel & Cromack 1977; Berg & Staaf 1980). The loss of litter mass takes place primarily by release of CO_2 and other waste products, spore production by microbes, and leaching by water of water-soluble substances (Berg & Söderström 1979).

Berg & Staaf (1980) and Berg (1984) found that the decomposition of needle litter can be divided into 2 phases. In the first phase, the decomposition rate is regulated by concentrations of nutrients in the litter and the second phase lignin decomposition rate is the regulating factor.

The aim here was to quantify aboveground litter input, to analyze the variation in rates of decomposition at different periods of time, to measure the length of fungus mycelium in the litter, and to compare litter decomposition models and accumulation of soil organic matter in a *Pinus taeda* forest.

2. Study area

The sampling area is located in an island in the Parana de las Palmas river near the confluence of the Parana and Uruguay rivers between the provinces of Buenos Aires and Entre Rios, Argentina (58°51′30″ W and 34°10′40″ S). According to Borello (1968), the Parana Delta is a geological unit of Mesozoic origin, which according to its structure, symmetry, tectonic control of faults, morphology and support, the River Plate estuary can be classified as an "alaucodelta" or lineal delta.

Its soil is alluvial, formed by sedimentary deposits on the natural levee ("albardon") which surround the islands. The soil *p*H is acid. The delta system is included in the Paranaense phytogeographical province in which the vegetation is composed of degraded marginal forest on the somewhat raised alluvial soils (natural levee).

There are large marsh communities in which grasses and sedges are predominant and also aquatic communities in which *Elodea sp.*, *Lemna sp.* and *Wolfia sp.* are characteristic (Cabrera 1968). In 1966, an experimental *Pinus taeda* plantation was established on the natural levee. The trees were planted 3.5 miles apart. Variation of temperature and rainfall during the time and the location where the experiment was carried out are given in figs. 1 & 2.

3. Methods

3.1. Leaf litter decomposition

Since the loss of dry mass can be used to reflect decomposition, the litter bag method was used to measure it (Suffling & Smith 1974); these were prepared as follows: Leaves of *Pinus taeda* were

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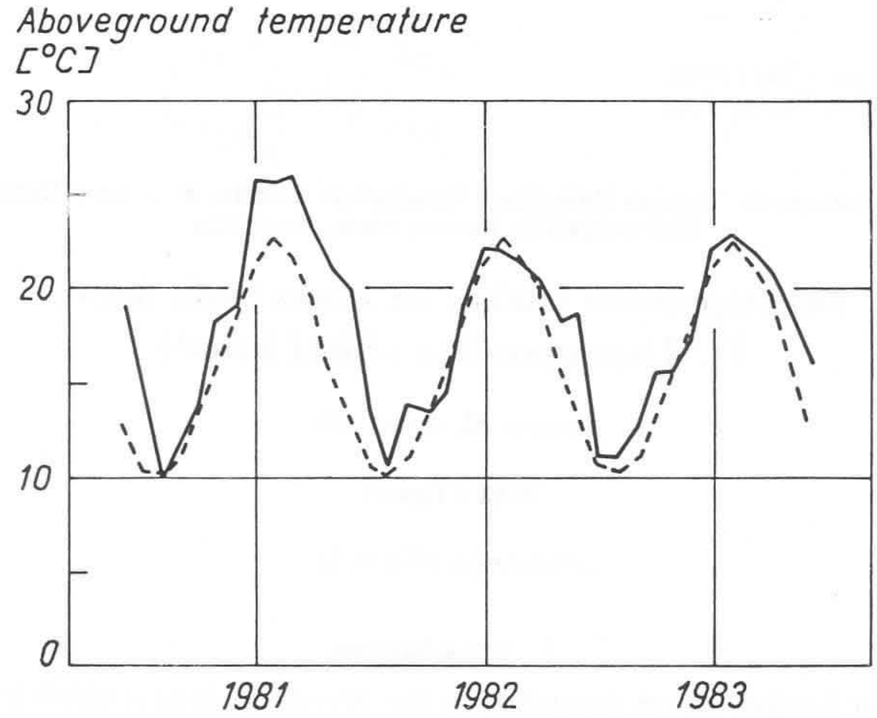

Fig. 1. Variation of rainfall during the time of the experiment in the area where it was carried out (———). [Mean values of rainfall 1942—1979 (- - - - -)]. These data were taken at the weather station of INTA Delta Experimental Station.

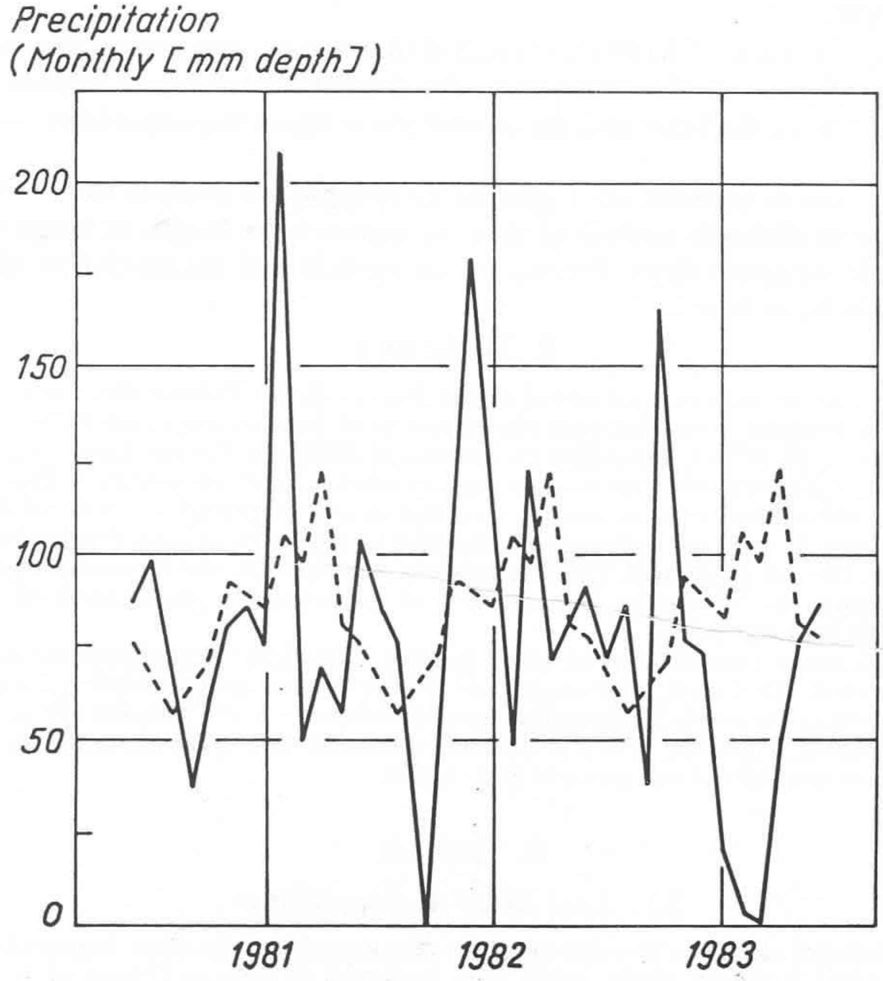

Fig. 2. Variation of aboveground temperature during the time of the experiment in the area, where it was carried out (———), [Mean values of temperature 1942—1979 (- - - - -)]. These data were taken at the weather station of INTA Delta Experimental Station.

caught in a net, air dried to constant mass for 3 weeks (at 25—28 °C), enclosed in plastic litter bags (5 g of needles in bags of 2 mm nylon mesh, 10 cm × 30 cm), and dried for an additional week. One hundred bags of pine litter were prepared and set out in the field study plot (40,000 m^2). Before field incubation, 5 bags were taken at random, oven-dried at 80 °C for 48 h and the oven dry mass [≙ xeromass (m_x)] correction factor was determined (11.12 ± 0.35) (X ± SD). All mass values are gram dry mass equivalents.

The litter bags were placed among the freshly fallen litter in the main field plot about two months after the maximum litter fall, and bags of litter were sampled at approximately 3 month intervals after placement in the field on May 12, 1980. At each sampling time, 5 litter bags were collected, transported directly to the laboratory and cleaned of plant remains (roots, grasses, etc.). The loss of dry mass of the needles was determined by difference between initial dry mass and final dry mass.

3.2. Leaf litter input

Four litter traps were randomly placed in the main study area for the duration of the study period (3 years). These traps consisted of metallic containers (30 cm diameter) lined to half their depth (about 50 cm) with a plastic net to allow the drainage of rainwater. Leaf litter was collected every month. Dry masses of the collected needles are given in Table 1.

Table 1. Above ground litter input for a *Pinus taeda* forest

Month	Litter input $g\ m^{-2}$	Month	Litter input $g \times m^{-2}$
September	26.14 ± 3.4	March	163.05 ± 17.5
October	22.65 ± 2.1	April	35.73 ± 2.8
November	25.29 ± 1.8	May	183.23 ± 5.1
December	33.09 ± 3.9	June	81.86 ± 2.3
January	108.56 ± 6.9	July	15.99 ± 2.1
February	72.51 ± 1.4	August	27.68 ± 1.1

3.3. Estimation of fungal biomass

Quantitative assessment of fungal mycelium was made from three litter bags at each sample time. One gram of leaf sample was fixed in Boudin Hollander fixative and macerated in a blender for 10 min. The suspension was warmed to 50 °C and 50 ml were diluted with molten agar solution (final concentration 1.25%) and kept at 50 °C in a water bath.

Ten soil agar films were made from each suspension in haemocytometer slides (0.1 mm depth). After the films had solidified, they were transferred to glass slides, dried, and then mounted in glycerine jelly. The unstained films were observed under a phase contrast microscope (Wild M-20) at 400 × magnification and the fungal lengths were measured by the intersection method (Olson 1950). Twenty microscopic fields were counted for each slide (Jones & Mollison 1948).

3.4. Leaching experiments

Release of water soluble substances from the whole needles was investigated by allowing the needles to soak in distilled water at room temperature for 24 h. After soaking, the mass was determined after drying at 80 °C.

3.5. Pattern for needle litter in the L layer

Calculations were carried out only for the L layer, the aim being to determine the amounts of needle litter biomass and some main flows in this layer.

The calculations were carried out from the yearly inputs of needle litter (Table 1). The mass of needles stored in the L layer was taken from direct measurement (numbers between parentheses) and calculated from differences between litter input and mass losses given in Table 2.

4. Results

4.1. Leaf litterfall and dry mass loss

In a *Pinus taeda* forest in Argentina, leaf litter falls throughout the year (Table 1) with the highest values in March (Autumn) and the lowest in June (Winter); after 6 months all the litter bags had been covered with new leaves. Because of the occurrence of high winds at various times of the year, the input of leaf litter showed differences during the same months

Table 2. Dry mass loss percentage (± 95% confidence limits) and decomposition parameters for leaf litter decomposition in a *Pinus taeda* forest (t_0 = 4-12-1980) (2 mm mesh bag)

Decomposition time (days)	Dry mass loss %	K	K′	T_{50} days	T_{99} days
98	9.54 ± 5.23	0.293,9	0.094,8	677	4,501
197	14.83 ± 2.37	0.301,4	0.148,3	842	5,645
297	22.56 ± 1.75	0.321,4	0.225,6	823	5,505
373	28.74 ± 2.69	0.335,3	0.287,4	786	5,236
456	48.18 ± 6.32	0.539,0	0.481,8	587	3,693
562	44.13 ± 10.52	0.376,7	0.441,3	621	3,975
664	52.97 ± 5.64	0.415,0	0.529,7	617	3,943
751	72.81 ± 4.08	0.636,5	0.728,2	532	3,140
840	51.38 ± 3.13	0.309,9	0.513,8	588	3,725
946	64.99 ± 2.07	0.394,2	0.649,9	599	3,851
1,043	62.85 ± 2.50	0.331,0	0.628,5	624	4,164

$k = \ln \frac{x_0}{x_t}$ and $k' = 1 - \frac{x_t}{x_0}$, where

x_0: initial mass of litter (t_0)
x_t: mass of litter at time t
T_{50}; 50% decomposition time in days
T_{99}; 99% decomposition time in days

in each of the 3 experimental years (1980—1983) (Table 1) at which time green leaves also appeared on the forest floor.

Whole needles of *Pinus taeda* did not leach significant amounts of water-soluble substances [24 h incubation in distilled water gave a mass loss of 0.9 ± 0.08 ($\bar{X} \pm$ SD)]. Needles have an outer layer of epidermis with a strong layer of cutin which impedes the leaching of water-soluble substances (NYKVIST 1963). Thus, almost all mass loss must be due to the effect of biotic decomposition. In the needle litter, there was little leaching initially, but it increased when the needle structure was physically and chemically broken down.

Using dry mass loss, various authors have attempted to use mathematical models to describe plant litter decomposition (OLSON 1963; BUNNEL & TAIT 1974; HOWARD & HOWARD 1974). *Pinus taeda* leaf litter decomposition responded as a negative exponential function:
$m(t) = m_0 e^{-rt}$ with the following values:
$m = 99.63\, e^{-0.001t}$ $r = 0.88$ $n = 12$ $p = 0.05$.

Losses in dry mass of leaf litter over the first 33 months and the calculated decomposition parameters are given in Table 2.

Using dry mass loss and leaf litter input, changes in the L layer litter and humus formation during the year were calculated (Fig. 4) and checked by measurements in the field. Small differences were found between calculated and observed data, probably due to differences in water content of confined and unconfined litter (Table 4). Using Scanning Electron Microscopy (SEM) at different degrees of decomposition, only mycelium of fungi and *Thecamoebas* could be observed (Fig. 3).

4.2. Fungal biomass

The newly fallen *Pinus taeda* needles contained few microorganisms (4.37 ± 0.82 mg^{-1} dry mass). During the first months in the field, the fungal biomass increased slowly. Between November and May, during the first year, a strong fungal growth took place, increasing the mycelial length from 4.28 ± 0.89 mg^{-1} m_x to 23.36 ± 0.86 mg^{-1} m_x (Table 5). During the first phase of decomposition, and until water content of the sample reached an approximate value of 60%, the total length of mycelia was correlated with the moisture present in the sample. This fact has also been recorded by BÅÅTH & SÖDERSTRÖM (1982). After having been in contact with the soil for one year, the water content of litter remained between 58.85 ± 2.5 and 69.34 ± 2.4%, in spite of the fact that this amount of mycelium varies with a peak in Autumn and decreases toward Summer.

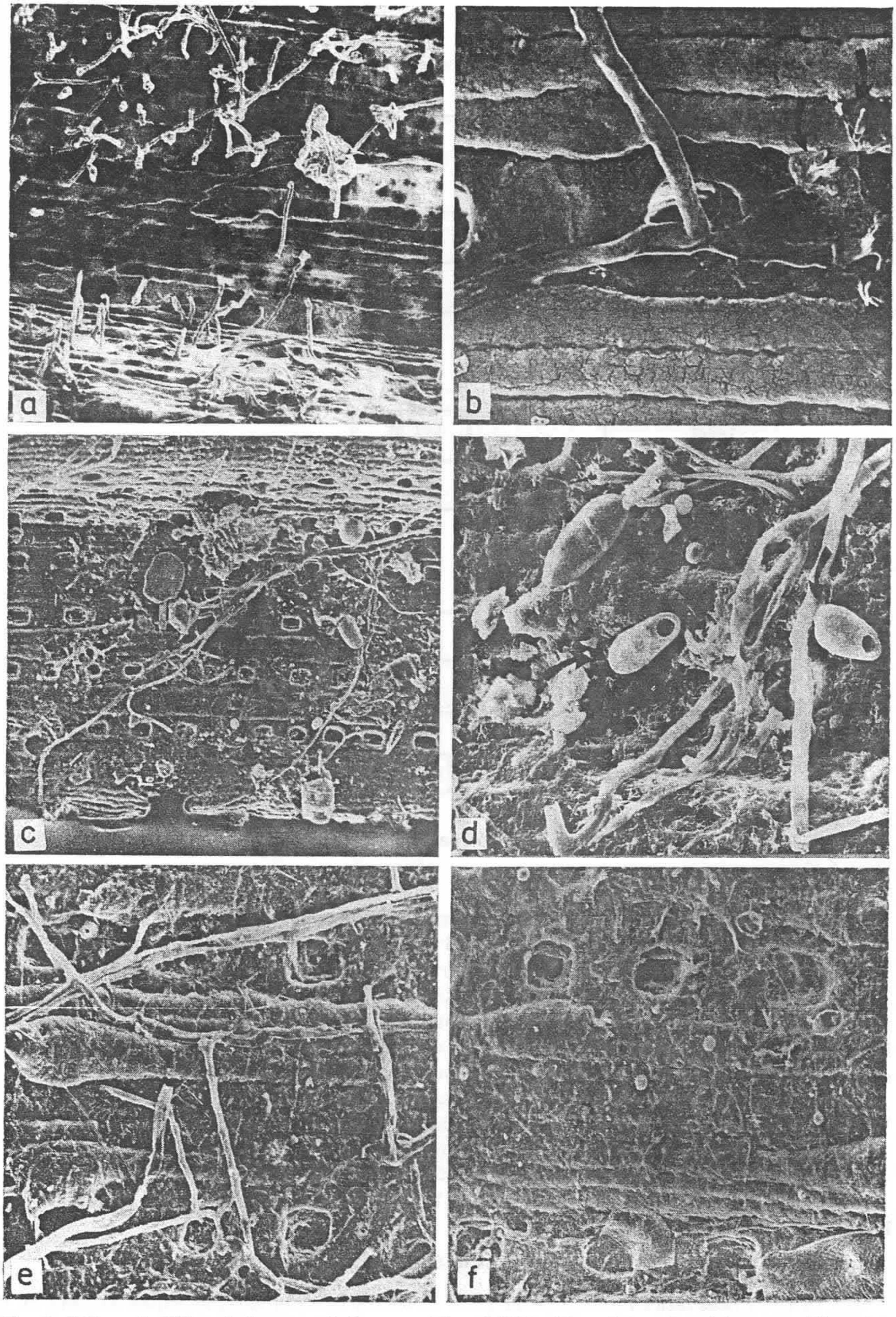

Fig. 3. Litter at different degrees of decomposition (SEM). After 6 months of decomposition: (a) 3000×, (b) 6000× (arrows show appressoria of fungi). After 12 months of decomposition: (c) 3000×, (d) 6000× (arrow shows Thecamoeba). After 18 month of decomposition: (e & f) 6000×, mycelia and bacteria.

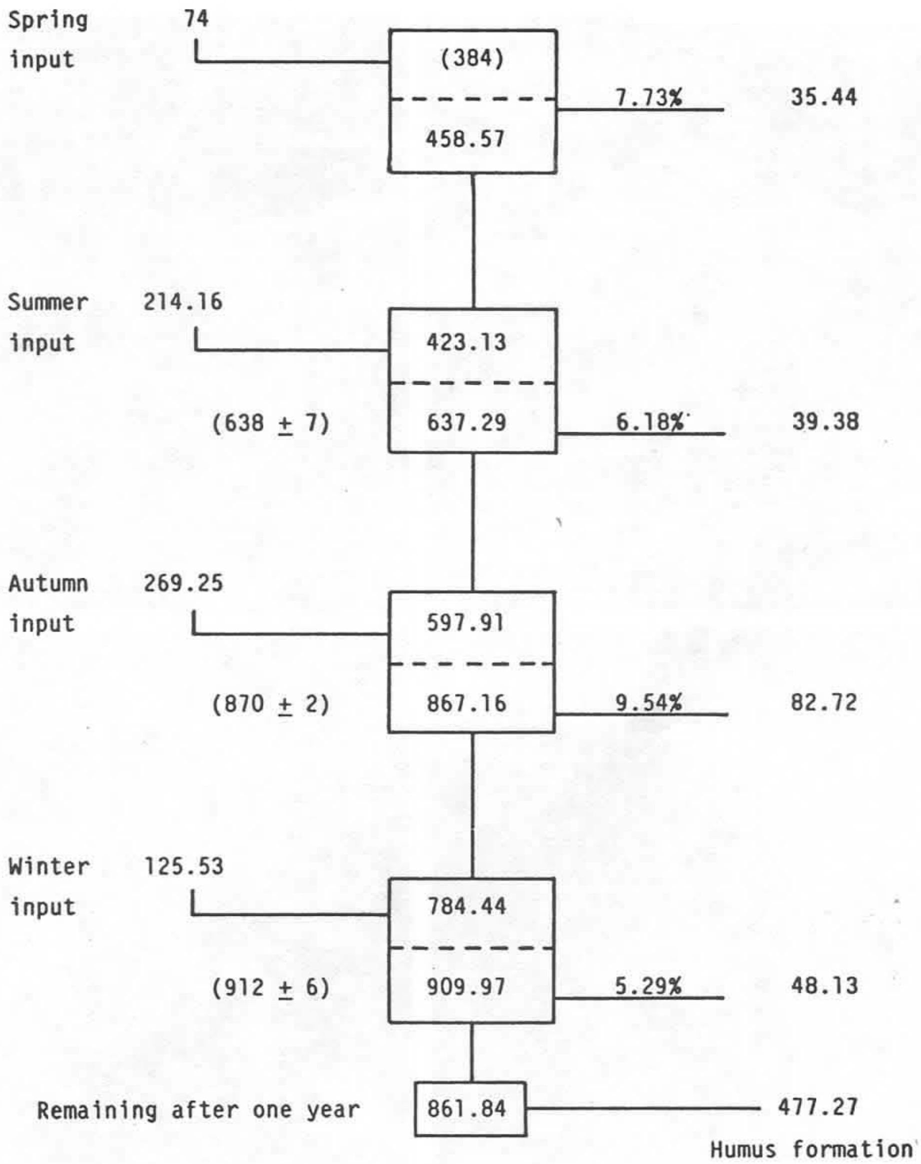

Fig. 4. Changes in mass of the L layer litter compartment over a year in a *Pinus taeda* forest (Value are g × m^{-2}).

The maximum values for each year progressively decreased (May 1981, 23.36 ± 0.86; May 1982, 10.14 ± 2.8; May 1983, 7.4 ± 0.76 mg^{-1} m_x). This can be interpreted as follows. The fungal mycelium upon invading litter grows, using available soluble substances and its development takes an ascendent value. When those nutrient substances decrease, fungi utilize insoluble ones, such as cellulose and lignin, abundant in the plant tissue. Both are linked to form part of cell walls and are impossible to degrade independently. The degradation products of lignin can react with nitrogen compounds of the leaf, thus limiting the quantity of nitrogen available for microorganisms and retarding mycelial growth (Bååth & Berg 1982). In the Autumn of each year, there is an important addition of leaves to the ground; when attacked by microorganisms, they add soluble substances to the medium, making possible the growth peak in the mycelium colonizing the litter. This peak is progressively less pronounced due to the slow relative enrichment of lignin regarding cellulose, which retards mycelial growth in the litter.

5. Conclusions

(1) In the *Pinus taeda* forest, 688.34 g m^{-2} of leaves fall annually, of which 477.24 g m^{-2} are incorporated in soil as humus.

Table 3. Comparison of annual decomposition rate (k) for a variety of coniferous leaf litter

Tree species	k	References
Abies amabilis	0.56	Turner & Singer 1976, WA
Pinus jeffreyi	0.11	Stark 1973, NV
Pinus strobus	0.42—0.52	Cromack 1973, NC
Pinus sylvestris	0.352	Berg & Wessén (in press) Sweden
Pinus taeda	0.51—0.58	Sollins *et al.* 1973, TN
Pinus taeda	0.33	Godeas (present study). Argentina
Pinus virginiana	0.45—0.46	Sollins *et al.* 1973, TN
Pinus sp.	0.31	Mikola 1960, N. Finland
Pinus sp.	0.43	Mikola 1960, S. Finland
Pseudotsuga menziensii	0.22—0.31	Fogel & Cromack 1977, OR

Table 4. Moisture in confined and unconfined *Pinus taeda* litter during the present study

	Confined litter	Unconfined litter	
		L horizon	H horizon
Initial	11.12 ± 0.35		
1st year	69.34 ± 2.4	14.17 ± 0.86	66.15 ± 2.7
2nd year	69.34 ± 2.4	19.15 ± 1.30	60.83 ± 3.4
3rd year	63.08 ± 4.3	12.16 ± 2.0	65.17 ± 5.4

Table 5. Variation of moisture contents and total length of mycelia during the *Pinus taeda* leaf litter decomposition experiment

Decomposition time (days)	Moisture %	Length of mycelia m × g^{-1} dry mass
0	11.12 ± 0.35	4.37 ± 0.82
98	18.82 ± 1.40	5.14 ± 0.83
197	14.54 ± 0.7	4.26 ± 0.98
297	20.53 ± 0.68	7.65 ± 0.99
373	69.34 ± 2.4	23.36 ± 0.86
456	61.90 ± 8.02	19.07 ± 1.19
562	67.89 ± 3.81	5.83 ± 1.02
664	66.62 ± 2.33	3.45 ± 0.4
751	63.08 ± 4.19	10.14 ± 2.8
840	68.69 ± 1.53	6.41 ± 1.1
946	67.84 ± 1.90	4.32 ± 0.12
1,043	58.85 ± 2.5	2.27 ± 0.64
1,133	68.03 ± 4.3	7.40 ± 0.76

Note: Moisture content is percentage of oven-dry mass at 80 °C.

(2) Mass loss through leaching was estimated as 0.9 ± 0.08 % per 100 g after one day of soaking in destilled water at room temperature. Thus, it is necessary that the leaf structure be attacked by microorganisms so that mass loss may occur.

(3) Rate of decomposition (k)*) was calculated as 0.33 and dry mass loss took place in an exponential equation ($m = 99.63\ e^{-0.001t}$).

(4) Length of mycelia in the leaf at the time of leaf fall is 4.87 ± 0.82 $m \times g^{-1}\ m_x$ litter and its moisture 11.12 ± 0.35 %. Litter, when in contact with soil, increases in moisture and is colonized by soil microorganisms that slowly destroy the leaf structure.

Length of mycelia increases until it reaches the maximum value recorded in this study, 23.36 ± 0.86 mg^{-1}, and then begins to decrease, with periodic peaks. These coincide with Autumn, the time at which there is a greater deposition of litter on the soil and, therefore, a larger amount of available nutrients.

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*) $k = \ln\left(\frac{x_0}{x_t}\right)$

(5) Moisture in confined litter bags is slightly larger than for unconfined litter and varies between 69.34 ± 2.4 and 58.85 ± 2.5%. Length of mycelia in litter after this has become colonized by soil fungi is modified by moisture.

(6) Direct observation of litter made by SEM in different stages of decomposition reveals only surface mycelium, bacteria and *Thecamoebas*.

6. Acknowledgements

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Synopsis: *Original scientific paper*

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Studies on litter decomposition using decomposition bags were undertaken. The following parameters were measured: **(a)** mass loss resulting in a curve which responds to the equation $M = 99.63\ e^{-0.001t}$; $r = 0.88$, $n = 12$, $p < 0.05$, with the rate of decomposition (k) 0.33 $\left[k = \ln\left(\frac{x_0}{x_t}\right)\right]$. This curve is more influenced by moisture than by temperature; **(b)** with this data and the amount of fallen leaves (683.34 $g\ m^{-2}$), the incorporation of organic matter in the soil was calculated (299 $g \times m^{-2}$); **(c)** By direct observation with SEM, it was determined that the most important decomposer organisms are fungi and *Thecamoebas;* **(d)** measurement of the fungal biomass indicated that the maximum length value is reached after one year (23.36 $m \times g^{-1}\ m_x$ litter).

Key words: Litter decomposition, fungal biomass, dry mass loss, *Pinus taeda*